
WEEDS IN PARADISE: THOUGHTS ON THE INVASIBILITY OF TROPICAL ISLANDS¹

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ABSTRACT

Tropical island ecosystems appear to be especially vulnerable to invasive species as indicated by the often high numbers and percentages of exotic species on oceanic and continental islands. Here I reexamine hypotheses offered to account for the apparently high invasibility of tropical islands and suggest a simple synthesis based on resource availability, propagule supply, and relative competitive abilities of exotic and island species. This review suggests that fundamentally two interacting processes—high net resource availability and poor ability of native species to preempt those resources—make island communities vulnerable to the establishment and spread of alien species. In addition, historically high rates of introduction have provided opportunity in the form of a diverse and abundant propagule rain of exotic species. The combination produces a scenario that is not an optimistic one for island ecosystems. It suggests that these native ecosystems on islands are particularly vulnerable to naturalizing exotics growing on their borders, and that while disturbance from a variety of causes, including pigs, fire, grazing, and natural dieback of the canopy dominants, increases the opportunities for exotic incursions, even intact forests are not immune. Unless these forests are aggressively managed and alien propagule pressure reduced, they will be highly modified by expanding exotic plant populations. Tropical islands are an effective early warning system of the impacts that successive waves of exotic species invasions may cause to isolated ecosystems. As mainland natural areas become fragmented, degraded and depauperate, they acquire many of the ecological attributes of islands, including limited habitat area, missing functional groups, declining species diversity, and disturbed habitats. A better understanding of invasions on islands may improve our attempts to protect both mainland and island ecosystems from the impacts of exotic species.

Key words: alien species, exotic species, extinctions, invasive species, invasibility, island ecosystems, plant communities, tropical islands.

“He who admits the doctrine of the creation of each separate species, will have to admit that a sufficient number of the best adapted plants and animals were not created for oceanic islands; for man has unintentionally stocked them far more fully and perfectly than did nature”

—C. Darwin ([1859] 1972: 347–348)

Island ecosystems appear to be especially vulnerable to invasive species. Reviews cite the high numbers and percentages of exotic species on heavily visited oceanic and continental islands (e.g., Vitousek et al., 1997), and invasive species often are implicated in species extinctions in island ecosystems (Simberloff, 1995; D’Antonio & Dudley, 1995). Tropical islands as well often are characterized by high alien species densities, unlike tropical mainland ecosystems where the incidence of alien species is low (Rejmánek, 1996). The apparently high invasibility of islands might suggest that island ecosystems hold few lessons for the prevention and management of exotic species in continental ecosystems. However, as mainland natural areas become fragmented, degraded, and depauperate,

they acquire many of the ecological attributes of islands, including limited habitat area, missing functional groups, declining species diversity, and disturbed habitats (Laurance & Bierregaard, 1997). A better understanding of invasions on islands may improve our attempts to protect both mainland and island ecosystems from the impacts of exotic species.

Here I reexamine hypotheses offered to account for the apparently high invasibility of tropical islands and suggest a simple synthesis based on resource availability, propagule supply, and relative competitive abilities of exotic and island species. My focus is on invasions of exotic terrestrial plants into native island ecosystems. In the following discussion, I describe some of the hypotheses proposed to account for variation in community invasibility; however, in developing the synthesis I have relied on few assumptions about the presence of vacant niches or the strength of competitive interactions in equilibrium communities. Rather, I assume that ecological communities are open to the

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establishment and evolution of new species and that they are constantly changing with variation in the environment and in the abundance of competitors, mutualists, diseases, and predators (Hubbell, 2001). The composition and structure of plant communities seem largely attributable to differential responses of individual species to resource availability, habitat conditions, and pest pressures. Beyond these individualistic patterns, assembly rules for plant communities are poorly understood and difficult to demonstrate (Wilson, 1999). Thus, I assume that some degree of invasibility characterizes all communities and that our challenge is to understand why some communities appear to be more open to the establishment of new species than others.

As D'Antonio and Dudley (1995) observed, generalizations about the vulnerability of islands to invasive species often fail to distinguish among invasibility, opportunity, and impact, any or all of which may contribute to observed patterns: (1) island communities may be more *invasible*, that is, with similar opportunity exotic species may be more likely to establish new populations in island than in mainland communities; (2) the *opportunity* for new colonists may be greater on islands because islands may be exposed more frequently to inputs of seeds and other propagules than mainland habitats; and (3) the *impact* of exotic invasions on island species and ecosystems may be more substantial than on similar mainland communities.

Both opportunity and impact are high on many tropical islands. Because islands often lack critical sources of food, forage, and fiber, colonists from early Polynesian voyagers to modern government agencies have promoted plant introductions, including pasture grasses, timber trees, food crops, ornamentals, and sources of fuel and fiber (Mueller-Dombois & Fosberg, 1998). In addition, rates of unintentional introductions are often high because islands have been important provisioning stations for transoceanic shipping traffic, exposing island habitats to species from wide and heterogeneous sources. Moreover, invasive species have strong impacts on islands, because the spatial extent of ecosystems and the population sizes of species are necessarily small and thus vulnerable (Simberloff, 1995, 2000; Sakai et al., 2002). Here I focus on the *invasibility* of tropical island ecosystems and ask whether community processes on islands make them particularly vulnerable to the establishment and spread of alien species and, if so, whether these observations have broader implications for our understanding of invasion ecology.

ARE ISLAND COMMUNITIES MORE INVASIBLE?

Ecological and evolutionary theorists have suggested several factors that may make island communities particularly vulnerable to the establishment of novel species. Communities with low native species diversity, missing functional groups, disharmonic community composition, poorly competitive species, and low pest pressures are seen to provide few barriers to the establishment of mainland species adapted to ecosystems with higher pressures from competitors, predators, and pests (Rejmánek, 1996; Simberloff, 2000; Mack et al., 2000).

LOW DIVERSITY ON ISLANDS

The effect of native species diversity on the invasibility of island communities is predicated on two hypotheses: (1) that there are fewer species on islands than in mainland habitats of comparable size, and (2) that high species richness is a deterrent to the establishment of alien species (Elton, 1958). The proposition that islands are less diverse than mainland areas of comparable size comes largely from island biogeography theory (MacArthur & Wilson, 1967), which proposes that two interacting processes affect species richness on islands: The distance of islands from mainland source pools affects immigration rates of new species, and island size affects the number of species of minimum viable population sizes that can be accommodated. Thus diversity on small and/or remote islands is likely to be lower than in mainland habitats of comparable size (MacArthur & Wilson, 1967).

Island-mainland comparisons of native plant species diversity are scant, however. Frequently cited support for the pattern of low plant diversity on islands is still MacArthur and Wilson's original treatise, although often the generalization is regarded as sufficiently widely recognized as to need no documentation. However, many factors affect native plant diversity on islands, and their effects are not easily separated (Carlquist, 1974). Geological age, latitude, elevation, habitat diversity, productivity, and proximity to source pools all affect rates of immigration and diversification as well as patterns of species coexistence (Ricklefs & Schluter, 1993; Simberloff, 2000). Early human settlers on oceanic islands not only brought new species, but caused such widespread extinction and habitat alteration that native lowland floras in particular are difficult to reconstruct (Steadman, 1995; Kirch & Hunt, 1997; Mueller-Dombois & Fosberg, 1998). These factors interact to produce high variation in species richness among islands and mainland sites and to

obscure effects of isolation and area on diversity. At least one study suggests that islands may not be significantly less rich than mainland sites. Lonsdale (1999) found no difference in the species richness of island and mainland native floras from 104 island and mainland sites after area was taken into account. Similarly, syntheses of earlier studies suggest little difference between species-area curves for island and mainland sites (Rosenzweig, 1995), and low regression coefficients in species-area plots of island plants suggest that correlates of species diversity are more varied than can be accounted for by area and isolation alone (Gilbert, 1980). Island floras may not always be more species poor than those of mainland habitats.

If species diversity is assessed at the patch or stand level where most ecological interactions take place, low diversity may be a salient aspect of island ecosystems nevertheless. Island floras often are characterized by high levels of endemism. Even within archipelagos, ranges of congeneric species are often distinct and restricted to single islands, mountains, or valleys (Carlquist, 1974; Eliasson, 1995; Wagner et al., 1999). Although a few species are widespread and polymorphic, many have highly restricted, non-overlapping ranges. For example, speciation within Hawaiian *Cyrtandra* (53 species, Gesneriaceae), a genus of deep ravines and gulches, appears to have been driven by the isolation produced by the dissected topography of highly eroded islands (Carlquist, 1974). In most mainland tropical and subtropical forests, in contrast, within-stand diversity is high (e.g., Heaney & Proctor, 1990), characterized by high diversity within families and co-occurrence of many congeneric species (Croat, 1978; Hartshorn & Hammel, 1994). Thus at a stand level, if not at a regional level, species diversity is likely to be low in island ecosystems.

The thesis that species-rich communities are less invulnerable than species-poor communities was first suggested by Elton (1958) and has become a central tenet of invasion ecology (e.g., Mack et al., 2000). However, empirical support for this hypothesis seemingly has been ambiguous. At the landscape and regional scales, several recent analyses have shown that the most diverse communities often also have the largest number of exotic species. Analyses of islands (Lonsdale, 1999), riparian ecosystems (Levine, 2000), and rangelands (Stohlgren et al., 1999) all show strong positive correlations between native and exotic species diversity. The authors conclude that likely the same factors that promote a rich assemblage of native species—largely availability of limiting resources—also facilitate the establishment of exotics. In contrast, ex-

perimental manipulations of species in plots or microcosms suggest that more diverse assemblages may exploit resources more efficiently and resist establishment of new species (e.g., Levine & D'Antonio, 1999; Levine, 2000; Naeem et al., 2000; Tilman et al., 2001; Kennedy, 2002). These apparently inconsistent results from experimental and observational studies may be resolved by considering process and scale (Levine & D'Antonio, 1999). Both net resource availability and species richness may increase along a resource supply gradient if supply increases faster than uptake by the community (Fig. 1). Thus the effect of diversity on biotic resistance to invasions should be assessed in the context of resource supply and demand; net resource availability rather than species richness *per se* likely determines community invasibility (Shea & Chesson, 2002). For example, low diversity forests at Semliki Forest Reserve, Uganda, were found to be no more invulnerable than high diversity stands (Rejmánek, 1996). Similarly, observations of Davis et al. (1998) showed that competition intensity between tree seedlings and herbaceous vegetation was correlated with net resource supply rather than biomass or gross resource supply. These studies suggest two correlates of community invasibility: (1) new species are most likely to become established where limiting resources are available; (2) more resources are likely to be used or preempted when species richness is high than when it is low. Under conditions of constant resource supply, high species richness may reduce invasibility (e.g., Levine & D'Antonio, 1999; Tilman et al., 2001). On oceanic islands, low stand-level diversity likely contributes to low levels of resource use, high resource availability, and poor resistance to the establishment of new individuals (e.g., Kitayama, 1996; Kitayama & Itow, 1999).

DISHARMONIC FLORAS

In addition to their effects on species diversity, long-distance oceanic dispersal and novel environmental conditions constitute a strong ecological filter on island biota. As a result, insular floras are often depauperate in certain taxonomic lineages, functional groups, life forms, dispersal characteristics, or environmental adaptations, a pattern that Carlquist (1974) described as disharmonic. For example, rain forests on oceanic islands may lack tall, large-seeded, shade-tolerant canopy trees that dominate many mainland rain forests. In Hawaii, native palms are confined to a single genus (*Pritchardia*); in contrast, dwarf, understory, climbing, and clonal palms are common in mainland forests. Similarly,

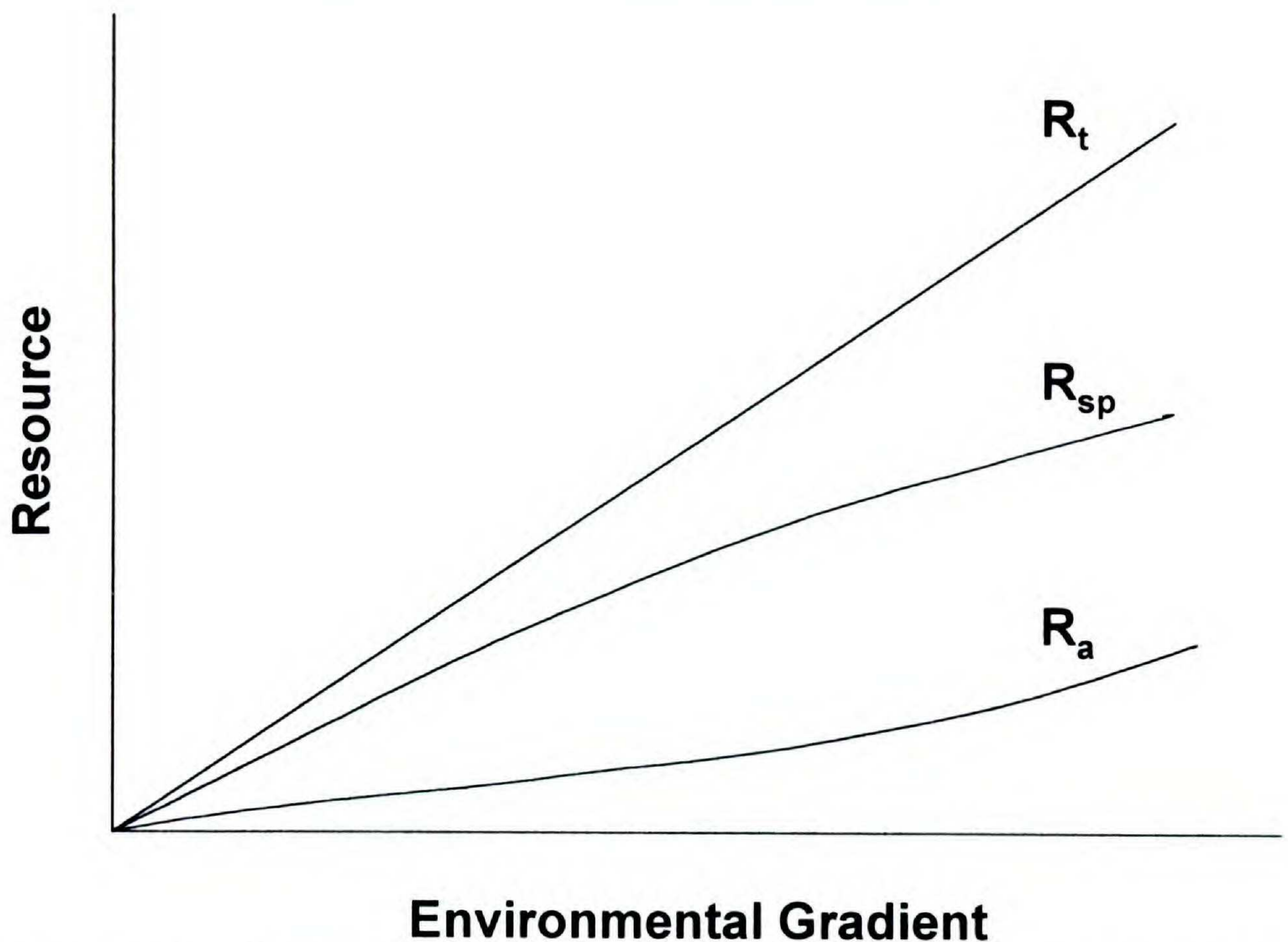


Figure 1. Hypothetical patterns of resource supply and demand across an environmental gradient. R_t = total resource availability; R_{sp} = resources consumed or preempted by species present. The increased resource demand reflects combined effects of all co-occurring species, which may often, but not always, be associated with an increase in species richness, functional group diversity, and/or redundancy within functional groups. R_a = available or net unused resources; these may remain unused or be exploited by additional native or alien species.

there are few species of native lianas in Hawaii. In mainland ecosystems, both of these functional groups can have important effects on forest structure and regeneration processes (Dewalt et al., 2000; Schnitzer et al., 2000; Farris-Lopez et al., ms.).

The availability of vacant niches arising from this disharmony in the structure of island biota is cited frequently as providing opportunity for invasive species (e.g., Mack et al., 2002; Shea & Chesson, 2002). Among plants, however, the concept of functional groups may be a more useful model than niches, since unique habitat and resource requirements are difficult to describe among plants. Species in a functional group share traits that similarly affect ecosystem and community processes (Fownes, 1995; Denslow, 1996). For example, *Myrica faya* Aiton (Myricaceae) is an alien, N-fixing tree that invades recent lava flows in Hawaii. Addition of its N-rich litter increases nutrient supply rates to other species and thus alters successional dynamics on this new substrate (Vitousek et al., 1987). The scarcity of native species that fill this role suggests that this functional group is missing in Hawaii (Fownes, 1995), although the presence

of widespread N-fixing shrubs in the fossil record (James, 1995) indicates that this role once may have been filled. Indeed the ability of alien invasive species to alter nutrient supply, disturbance regimes, light environments, productivity, and other ecosystem properties may be taken as evidence of unexploited opportunity and missing or poorly represented functional groups. Similarly, Kitayama (1996) and Kitayama and Itow (1999) suggested that low stand productivity and low above-ground biomass in spite of high resource availability were linked to low species diversity and missing functional groups in Hawaii and the Galapagos. However, a deterrent effect of native species on the establishment of alien species with similar habitat requirements, resource needs, and growth forms may be difficult to demonstrate. In Hawaii, for example, much of the diversity among woody plants resides in understory shrubs, yet this group of plants also is well represented in the naturalized exotic flora.

High levels of apparent functional redundancy among plants in mainland rain forests suggest that there may be few barriers to the coexistence of many species playing similar functional roles. For

example, about 1700 species of vascular plants have been recorded in 1536 ha at the La Selva Biological Station, Costa Rica, of which there are 44 species of *Piper* (Piperaceae), 39 species of *Psychotria* (Rubiaceae), and 25 species of *Miconia* (Melastomataceae) (Wilbur, 1994), almost all of which are understory shrubs and small trees. There are 107 species of lianas and 323 species of trees (Hartshorn & Hammel, 1994; Wilbur, 1994). Differences among these species, for example, in light requirements, growth form, or climbing mechanisms, are small, suggesting strong overlap among them in habitat requirements. In addition, studies on the 50-ha permanent plot in Panama fail to reveal significant habitat differences among the majority of coexisting trees and shrubs there (Hubbell et al., 1999; Harms et al., 2001). These patterns in relatively homogeneous forests suggest that the presence of many ecologically similar species is not a strong deterrent to the occurrence and persistence of plant species in mainland tropical forest. In this context, it also seems unlikely that the presence of native species would be a significant barrier to the establishment of ecologically similar alien species in island ecosystems.

NATIVE SPECIES ARE POOR COMPETITORS

Native species on islands often appear to be poor competitors (Darwin, [1859] 1972; Carlquist, 1974). For example, wet and mesic forests throughout the Hawaiian archipelago are dominated by a single highly polymorphic species, *Metrosideros polymorpha* Gaud. (Myrtaceae). These *Metrosideros* forests are characterized by relatively open canopies, widely spaced crowns, and inefficient light absorption (Cordell & Goldstein, 1999). As a result, considerable light reaches the forest understory (Cordell & Goldstein, 1999), where native and alien grasses, herbs, and shrubs are able to establish. In addition, net CO₂ assimilation, leaf turnover, and growth rates of *M. polymorpha* are generally low (Burton, 1982; Burton & Mueller-Dombois, 1984), and *M. polymorpha* shows little plasticity in response to increases in light or nutrient supply (Cordell et al., 2001; Austin & Vitousek, 2000). Where growth or carbon fixation rates have been compared, lower rates are often measured in native Hawaiian than in comparable alien species (Pattison et al., 1998; Baruch & Goldstein, 1999; Durand & Goldstein, 2001). Similarly, the exotic Himalayan raspberry, *Rubus ellipticus* Sm., is replacing the native 'akala, *Rubus hawaiiensis* A. Gray, in the tree-fall gaps both require for establishment in montane rain forest. Although the two species have similar

dispersal mechanisms and habitat requirements, the alien *R. ellipticus* exhibits faster growth rates, a more efficient canopy configuration, and greater seed production increasing the likelihood that it eventually will replace the native species in these forests (Denslow, unpublished data).

The reasons why island species should be poor competitors are various. Loss of resilience in the gene pool may be a consequence of founder effects, inbreeding depression, small population sizes, strong post-establishment selection, drift, and low vagility of pollinators and dispersers (Carlquist, 1974; Loope & Mueller-Dombois, 1989; Kaneshiro, 1995). The steep environmental gradients over short distances that characterize high tropical islands may constrain development of specialized adaptations. For example, Kitayama (cited in Denslow, 2001) has suggested that the dominance of oceanic island forests by species with wide ecological ranges may be linked to their low productivity and high invasibility. In his study of Hawaiian and Bornean rain forests (Kitayama, 1996), he found that species on Borneo had narrower elevation ranges than did species in Hawaii. He suggested, therefore, that the Bornean species may be better adapted to their environments and thus present stronger barriers to alien species than the more broadly adapted species in Hawaii. The links among adaptive ranges, competitive ability, and resistance to invasion deserve further exploration in this regard. A large proportion of island endemics are threatened or endangered due in part to their small ranges (Simberloff, 2000; Sakai et al., 2002), and the positive correlation between range size and local abundance has been widely acknowledged (e.g., Brown & Maurer, 1984; Kelly, 1996). These studies suggest that on islands, depauperate and disharmonic floras and poorly competitive species may result in low productivity and high ecosystem invasibility.

Loss of dispersal efficiency in island species may contribute to their poor competitive abilities. The generality of this pattern in many unrelated plant groups (Carlquist, 1974) suggests that selective pressure to avoid loss of reproductive output and reduce investment in dispersal mechanisms is strong on islands. Compounding the evolutionary loss of dispersability has been the historic loss of avian frugivores in Hawaii (James, 1995), loss of pollinators, and lack of a persistent seed bank in many native species (Drake, 1998), all of which contribute to low seed availability. As a result, population growth of native species may be strongly dispersal-limited in some habitats. Indigenous species thus may be less likely to fully occupy suitable

habitats than aliens with better dispersal mechanisms, greater seed output, and larger seedbanks, and less likely to reach and occupy critical, but ephemeral, establishment sites such as treefall gaps and nurse logs. Dispersal limitation contributes to less-than-full exploitation of limiting resources in all ecosystems (Hubbell, 2001), but may be particularly important on islands.

EFFECTS OF LOW PEST LOADS

The enemy release hypothesis proposes that alien plant species in their introduced ranges experience lower pest loads than co-occurring native species and than they do in their native ranges (Keane & Crawley, 2002). As a result, populations of exotic species may be released from control by natural enemies, enhancing their competitive positions relative to native species, which may remain under pressure from specialist and generalist enemies. There have been few appropriate tests of this hypothesis and in a few cases only were significant impacts of either generalist or specialist herbivores on the exotic plant species recorded (Keane & Crawley, 2002). Classical biological control—the introduction of specialist pests and pathogens to control invasive species in their introduced ranges—is based on this premise. There are several examples of intentional and accidental introductions of pests limiting the populations of their hosts (Louda et al., 1997; Strong & Pemberton, 2000), and Louda (1982) and DeWalt et al. (unpublished ms.) offer evidence that pests limit both growth and habitat distributions of weedy plants. In addition, data presented by DeWalt et al. (unpublished ms.) suggest that survival of *Clidemia hirta* (L.) D. Don (Melastomataceae) is more strongly affected by insect and pathogen impacts in its native than in its introduced range. The role of pest and pathogen pressure in island plant invasions is still poorly understood.

Furthermore, indigenous island species, which also originated as waifs, are thought to be under low pressure from natural enemies as well (Carlquist, 1980). In the process of dispersal to new and isolated habitats, insular floras are thought to have left their specialized pests behind. While subsequent diversification has produced many specialized associations of plants and their natural enemies (Swezey, 1954), the common lack of defensive compounds and structures among indigenous island species suggests that plant pathogen and herbivore impacts are not high. As a result, island plants may be particularly vulnerable to the introduction of exotic pests such as ungulates (Mueller-Dombois &

Fosberg, 1998; Richardson et al., 2000). If islands are depauperate in natural enemies or dominated by specialist herbivores, both exotic and native species may be under little control by their natural enemies. The net effect of low pest loads on native and alien plant species on islands is then difficult to predict. We lack critical information on the role of natural enemies in limiting plant population growth, abundance, and distribution in both mainland and island habitats. On balance, however, the more rapid growth rates and plastic physiological responses of alien species may result in their greater population growth where pest pressures are low (Keane & Crawley, 2002).

SYNTHESIS

Net resource availability is an important component of community invasibility. The role of resource pulses in the spread of alien species has been noted widely (Vitousek et al., 1997; D'Antonio et al., 1999; Mack et al., 2002). The generality of this relationship can be extended usefully to include chronic as well as temporary resource availability, such as that provided by disturbances, and to affect native as well as alien species. Seedlings of both native and alien species are likely to become established where resources are chronically or temporarily under-used, as following natural or anthropogenic disturbance; under conditions of naturally high levels of resource supply; where resources are incompletely exploited by the existing community; or where resource supply has been augmented. For example, it is widely recognized that both natural and anthropogenic disturbances facilitate the establishment of alien species (Rejmánek, 1989; Horvitz et al., 1998; D'Antonio et al., 1999), in part because disturbance reduces competition and increases local resource availability. In intact native communities, ant mounds, treefall gaps, and riparian habitats are important sites for seedling establishment (Platt, 1975; Denslow, 1987; Levine, 2000). Similarly, where disturbances are ecologically novel or unusually frequent or intense, we can expect that some native species as well as some exotic species may find suitable environmental conditions. Diversity and abundance of both alien and native species also are often highest in resource-rich habitats (e.g., Stohlgren et al., 1999), and, conversely, communities characterized by resource limitation (in Hawaii, alpine and subalpine ecosystems, communities on young lava flows, and dryland forests) are often notable for scarcity of exotic invasives. Other attributes proposed to increase community invasibility, such as

vacant niches, novel anthropogenic disturbances, or disequilibrium conditions, also address the availability of resource availability, but might be seen as special examples of a more general phenomenon.

In isolated tropical island habitats, resource availability likely is high because indigenous species do not effectively use or preempt them. Low local species richness, low diversity of functional groups, and low redundancy within functional groups suggest that few species may be available to take advantage of establishment opportunities or unused resources. Dispersal limitation, characteristic of all plant communities, may be particularly strong on islands, reducing the occupancy rate of suitable habitats and leaving sites and resources available for others. Where propagule pressures are high, the vulnerability of island communities to establishment of exotic species will be particularly apparent (Rejmánek, 1989; Drake, 1998; Levine, 2000).

Invasibility, however, is not a unilateral function of habitat characteristics, but rather the interaction of habitat and species. Limiting resources are available relative to the physiological and morphological capacity of plants to exploit them. Low growth plasticity in response to resource availability in many native species contributes to the underutilization of resources and thus invasibility of some island communities, and exotic species with more plastic growth responses may compete more effectively for natural establishment sites such as treefall gaps and decaying logs and take better advantage of novel disturbances such as pig foraging sites.

Assuming that fundamental tradeoffs between rapid growth rate in high light environments and persistence in shaded environments characterize alien and native species (Reich et al., 1997; Hubbell, 2001), both alien and native species should be able to thrive across a full spectrum of environments. Invasive species often are assumed to have characteristics of disturbance-adapted species (e.g., rapid growth in resource-rich environments and copious production of well-dispersed seeds); however, in part this pattern may reflect historic pathways of introduction associated with development of agriculture and rangelands (Mack, 1992), rather than inherent characteristics of invasive species. A rising global horticultural trade is introducing species that are shade-tolerant, spread vegetatively, and/or have large seeds (Reichard & Hamilton, 1997) and thus are potentially invasive in intact forest ecosystems.

This review suggests that fundamentally two interacting processes—high net resource availability and poor ability of native species to preempt those

resources—make island communities vulnerable to the establishment and spread of alien species. Historically high rates of introduction have provided opportunity in the form of a diverse and abundant propagule rain of exotic species. The combination produces a scenario that is not an optimistic one for island ecosystems. It suggests that these native ecosystems on islands are particularly vulnerable to naturalizing exotics growing on their borders, and that while disturbance from a variety of causes, including pigs, fire, grazing, and natural dieback of the canopy dominants, increases the opportunities for exotic incursions, even intact forests are not immune. Unless these forests are aggressively managed and alien propagule pressure reduced, they will be highly modified by new exotic introductions.

There are implications of this scenario for mainland ecosystems as well. With rising human populations, increased incursions into wilderness areas, and global environmental change, mainland preserves will assume many island-like characteristics. Habitat fragmentation and large-scale habitat loss will increase habitat isolation, reduce the extent, and increase the edges. Fragmentation of forests is widely associated with increased disturbance, alteration of edge and sometimes interior habitats, loss of species, and increased invasibility (e.g., Laurance & Bierregaard, 1997). Effects of population reductions and species extinctions will simplify ecosystem structure, reduce population sizes, produce disharmonies in species assemblages, and reduce functional redundancy. Loss of higher trophic levels, in particular, may result in increased populations of herbivores and edge species. Increased intensities and rates of exploitation will free resources (light, space, nutrients) and increase opportunities for exploitation by novel species. Rising rates of human traffic through suburban expansion, road extensions, global trade, ecotourism, and population movements will provide rising and repeated exposure to a diverse seed rain from exotic species. Tropical islands are an effective early warning system of the impacts successive waves of exotic species invasions may cause to isolated ecosystems. As island managers develop strategies for preventing and controlling these invasions, they will be watched by many on the mainland.

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